Phenology and phoretic bat mites of *Calyptrogyne brachystachys* (Arecaceae) flowers in the Monteverde Cloud Forest

Dylan J. Rhea-Fournier

Department of Ecology and Evolutionary Biology, University of Oregon

**ABSTRACT**

In November 2005 *Calyptrogyne brachystachys* palm inflorescences were examined for the presence of phoretic bat mites (tribe Melichari) in the Cloud Forest of Monteverde. Sixty-seven *Calyptrogyne brachystachys* plants were studied over a two-week period for flower and inflorescence phenology. Forty-six inflorescences were examined thoroughly for mite presence of which 11 were found to harbor mites. Flower phenology studies suggest a temporary flowering lag. Abundances of mites on both inflorescence and site scales were found at much lower frequencies than the Atlantic slope (Tschapka and Cunningham 2004), The lower abundance in Monteverde is attributed to abiotic differences such as recent weather patterns and biotic influences such as low flower abundance.

**RESUMEN**

Se examinaron inflorescencias de la palma *Calyptrogyne brachyrachys* en Noviembre del 2005 para determinar la presencia o ausencia de los ácaros foréticos en murciélagos (Tribu Melichari) en el bosque nuboso de Monteverde. Se estudiaron sesenta y siete plantas de *Calyptrogyne brachyrachys* por dos semanas para averiguar la fenología de las flores e inflorescencias. Once de las cuarenta y seis inflorescencias examinadas contenían ácaros. Los estudios de la fenología de las inflorescencias sugieren que hay un retraso temporal en la floración. Las abundancias de ácaros, examinadas por escala del sitio e inflorescencia, ocurrieron con frecuencias más bajas que en la Costa Atlántica de Costa Rica (Tschapka and Cunningham 2004). La abundancia más baja tal vez sea debida a las diferencias abióticas tales como patrones climáticos recientes e influencias bióticas como la baja abundancia de las flores.

**INTRODUCTION**

Commensalism when individuals of one species benefit from interactions with another species whose fitness does not change. Phoresy is a type of commensalism in which an organism travels on another solely for transport. This provides effective dispersal, particularly when the host animal predictably visits preferred patches frequently such as traplining nectavores or frugivores. (Boggs 1987).

A phoretic communalistic relationship occurs between hummingbirds, some hummingbird-pollinated flowers and a phoretic mite (Gamasidae: Ascidae). Up to 200 species of phoretic hummingbird mites have been proposed to exist in the closely related genera, *Rhinoseius* and *Proctolaelaps* (Hyneman at al. 1991). These mites can be seen with the naked eye and do not obtain any nutrients from the bird, relying on their hosts solely for transport/ dispersal, apparently disembarking in response to olfactory cues (Colwell 1983). The mites feed on nectar and pollen. These mites have been found to be extremely specific to floral hosts (Heyneman et al. 1991 found only 1 of 200 mites on a
flower host different than their regular hosts). Few flower hosts exist for a given mite species but presumably enough to provide year-round habitats. Heyneman et al (1991) also found that some hummingbird-pollinated flowers that meet all apparent criteria for mites are not colonized at all. This suggests high specificity and recognition of flower hosts among hummingbird mites as well as criteria still unknown, such as attractant or repellent properties of nectars (Heyneman et al. 1991).

Tschapka and Cunningham (2004) recently discovered a complex involving phoretic mites on Calyptrogyne ghiesbreghtiana (Areceae) and bats (Mammalia: Chiroptera) in La Selva, Costa Rica. Eight different species of bats were collected, including two nectarivorous bats (Phyllostomidae: Glossophaginae) and two genera of primarily frugivorous bats (Phyllostomidae: Stenodermatae); Artibeus and Carollia. Phoretic mites were only found Artibeus bats. Twenty-nine of 73 Artibeus bats collected carried mites and as many as 19 mites were found on one individual bat. Mites were found on the wing surfaces of the bats, in the same general region as where pollen is collected.

These mites (Tribe: Melicharini) were not found on any flowers other than Calyptrogyne ghiesbreghtiana. While hummingbird mites that have relationships with host plants that flower year round are monophagous, other hummingbird mites are polyphagous, having two or more hosts that they alternate due to seasonal phenology (Colwell and Naeem 1993). Tschapka and Cunningham (2001) found one species of flower pollen besides C. ghiesbreghtiana (Solanaceae: Markea neurantha) on Artibeus spp. harboring phoretic mites. Studies of M. neurantha and other bat-pollinated flowers have not yielded the presence of these mites, suggesting that these flower mites are truly monophagous.

The flowers that were studied for presence and colonization of mites excluded crawling mites by covering the peduncle of the inflorescence with glue. Seventy-six percent of the flowers surveyed were found to have flower mites.

Tschapka and Cunningham (2004) concluded that flower mites of C. ghiesbreghtiana used Artibeus bats as phoretic carriers. They went further in suggesting that mites were not found on other bats due to feeding behavior of the bats. Nectarivorous bats spend less than one second at each flower, while hummingbirds can hover for minutes. Frugivorous bats on the other hand perch to feed on nectar, allowing body contact with the inflorescence and longer visitation than hovering bats (Tschapka and Cunningham 2004).

Monteverde, Costa Rica is the home for populations of both frugivorous (18 species, mainly of the genera Carollia and Artibeus) and nectarivorous (7 species) bats (Timm and LaVal 2000) as well as Calyptrogyne brachystachys palms (Haber 2000). Artibeus toltechnus is the most abundant fruit bat in Monteverde, the primary pollinator of C. brachystachys species locally and is in the same genus as the bats found carrying mites in La Selva. Calyptrogyne brachystachys and C. ghiesbreghtiana are very similar and in fact Henderson et al (1995) describe the former as a higher elevation phenotype of the latter, with narrower leaflets and base constriction.

La Selva, Costa Rica is the first and only place that phoretic bat mites have been documented (Tschapka and Cunningham 2004), thus the geographical distribution of these mites are widely unknown. Given that Monteverde has similar species to those found in the La Selva, determining if a similar complex is present here in Monteverde is
imperative to broadening knowledge of bat mite biogeography. Furthermore due to abiotic differences between La Selva and Monteverde, confirmation of bat mite presence will shed light on how environmental factors affect colonization of these mites and what factors are limiting.

Elevation has potential effects on plant flowering phenology patterns and therefore colonization success of mites. The diversity of species involved in hummingbird-flower-mite complexes has found to decrease with elevation (Heyneman et al. 1991), implying a decrease in diversity in such relationships, and in parallel, bat-flower-mite complexes, in the higher elevation Cloud Forests in Monteverde.

Increased seasonality in Monteverde compared to La Selva may also impose influences onto the species interactions involved in a potentially bat mite complex. Seasonal changes in plant phenologies are likely to be greater on the Pacific side of the continental divide, possibly increasing seasonality of flowering patterns and associated folivores. In addition local weather patterns in Monteverde are much different than those found in La Selva. While both locations receive a substantial amount of rain, Monteverde also experiences periods of high wind and misty conditions. These types of weather patterns may very likely influence pollination, phoresy and bat activity.

The goal of this study was to reproduce Tschapka and Cunningham’s study at a higher elevation, within Monteverde Cloud Forest Reserve to determine if a phoretic mite – bat – flower complex exists.

METHODS

Study Sites
Fieldwork was conducted between November 3rd and 19th, 2005. Site 1 was located in a primary forest fragment between the Bullpen Pasture on the Campbell Property and “Windy Corner,” approximately 0.5 km from La Reserva de Monteverde, Costa Rica. This site experienced high frequencies of wind gusts, providing constant disturbance and resulting in low canopy trees.

Site 2 was located along the Quebrada Máquina off of the Sendero Jilguero behind La Estación Biológica de Monteverde, Costa Rica. This site consisted mainly of riparian habitats with a low canopy and thick understory.

Inflorescence Phenology Study
Fifty-one inflorescences at Site 1 and 11 inflorescences at Site 2 of Calyptrogyne brachystachys were monitored throughout the three-week study period at 2 to 4 day intervals. Only inflorescences that were pre-flowering were chosen for this study. Inflorescences were tagged and Vaseline was applied to the peduncle in order to exclude the introduction of any walking or crawling insects and/or colonization by crawling mites. The number of male and female flowers along with buds and location on the inflorescence were recorded during each date of collection.

Local Site Inflorescence Stage Survey
At each site a flowering stage survey was conducted to attain understanding of flowering stages of all inflorescences in the area. On November 16, 2005, 84 inflorescences were surveyed at Site 2 and on November 19, 2005, 145 inflorescences were surveyed at Site.
1. Inflorescences were categorized by the following criteria: Non-reproductive state (no inflorescence stalk present), unopened (spathe fully enclosing inflorescence), budding (spathe removed, but no flowers in bloom), flowering (any number of flowers present), post-flowering, fruiting and post-fruiting. Multiple inflorescences belonging to the same plant were counted separately.

**Analysis of Inflorescences for Mites**

Inflorescences monitored in the phenology study were collected when five to ten flowers remained or otherwise on the last day of study. Any additional inflorescences in flower, but not included in the phenology census, were also collected. Inflorescences were examined under an Olympus SZ40 dissecting scope for mite presence. Individual flowers were carefully dissected and floral pits investigated along the entire length of the inflorescence with a dissecting probe and knife.

**Bat Phenology**

Data for bat phenology were taken and graphed from Dienerstein (1983).

**RESULTS**

**Mite Occurrence**

Mites did not colonize the majority of the inflorescences examined. Eleven out of 46 inflorescences (23.9%) were observed to have the presence of mites (Fig. 1). A total of 36 mites were found on these 11 “mite-positive” inflorescences, with one inflorescence housing over 20 mites. This yielded an average of 3.27 +/- 5.59 mites per “mite-positive” inflorescence and an overall average of 0.78 +/- 2.99 mites (Table 1). While most mite-positive inflorescences had few mites, occasional inflorescences had many mites (Fig. 3 histogram). In respect to seasonality, more mites were found in inflorescences collected later in the study period (Fig. 2).

| Table 1. Inflorescence analysis of C. brachystachys for flower mites. n = 46. |
|---------------------------------|----------------------|
| Total mite abundance            | 36                   |
| Inflorescences containing mites | 11                   |
| Percent of inflorescences containing mites | 23.9%      |
| Mean number of mites per inflorescence | 0.78 ± 2.99 |
| Mean number mites per mite-positive inflorescence | 3.27 ± 5.59 |

Five of the 11 inflorescences found to harbor mites also exhibited chew marks, possibly evidence of bat visitation. In addition, six of the eleven inflorescences found to be colonized by mites had Vaseline applied to the peduncle prior to inflorescence opening to exclude crawling mites. This indicates that the colonizing mites arrived by air or a phoretic carrier.

Insect larvae (Arthropoda: Insecta) were found in 28% of the inflorescences surveyed with up to 5 larvae in one inflorescence. The presence of weevils (Insecta:
Scaribidae) feeding on flowers and surface worms (Annelida: Oligochaeta) feeding in floral pits were also observed.

FIGURE 1. Percentage of mite-positive inflorescences for each day of collection.

FIGURE 2. Histogram of frequency of bat mites on each individual inflorescence.
Plant Phenology
Phenology studies at both sites showed variation in frequency of C. brachystachyss inflorescences and flowers present each day. Trends in flower phenologies at site 1 are depicted in Figure 1. Over the two-week sampling period at site 1, the number of open inflorescences increases while the average number of flowers per inflorescence decreases. Site 2 showed an increase in frequency of open inflorescences and a corresponding increase in mean flower frequency per inflorescence (Fig. 2).

FIGURE 3. Phenology study at site 1 (n_{sample dates} = 5, i_{inflorescences} = 35 to 49). Frequency of open inflorescences increases slowly over a two-week period with the reciprocal decrease of unopened inflorescences. Interestingly the trend of average flowers per open inflorescence does not follow the trend of open inflorescences.
FIGURE 4. Phenology study at site 2 (n_{sample dates} = 2, n_{inflorescences} = 13). Frequency of open inflorescences increases over a one-week period with the reciprocal decrease of unopened inflorescences. Here the trend of average flowers per open inflorescence follows the trend of open inflorescences.

Local site survey of reproductive stages in *C. brachystachys* presented disproportionate frequencies in plant stages. Both sites were found to have low frequencies of inflorescences in budding and flowering stages in addition to individual fruiting or post-fruiting (Figs. 3 and 4). Many individuals were found to have unopened inflorescences, suggesting a high frequency of flowering individuals within the population in the near future.
FIGURE 4. Site 1, Bullpen fragment inflorescence stage survey (n = 145). Markedly more plants are in non-reproductive stages or have unopened inflorescence than any other, with inflorescences past the fruiting stage next common in frequency.

FIGURE 5. Site 2, behind La Estación Biológica de Monteverde (n = 84). Similar to site 1 (Fig. 2) and disproportional amount of plants have inflorescences that are unopened, post-fruiting or have no inflorescence stock at all.
Bat Phenology
Data taken from Dinerstein (1983) suggests seasonal phenology in *Artibeus toltecus* activity in the Monteverde Cloud Forest (Fig. 5). Bat activity in the area during the months of November and December are notably low.

![Image of a graph showing the phenology of *Artibeus toltecus* presence in Monteverde Cloud Forest. April 1981 to May 1982. Data from Dinerstein (1983).]


**Weather**
Local weather in the Monteverde Cloud Forest for the fall of 2005, occurring over the duration in which this study took place was exemplified by high winds, rain and mist (Fig. 6).

The mean rainfall for the month of October taken between 1952 and 1992 was 425 mm (Haber, 2000), while October 2005, the month preceding this study had a mean rainfall of 908 mm, including 22 days with greater than 10 mm of rainfall a day and 17 days with more than 20 mm of rainfall a day. In addition to these data, personal observations document high occurrence of mist and gusts in the evenings of November 2005.
FIGURE 6. Weather for Monteverde, Costa Rica. October 1st through November 19th, 2005

DISCUSSION

Phoretic flower mites were found on *Calyptrogyne brachystachys* inflorescences in Monteverde that had Vaseline applied to the peduncle, confirming arrival by air. Mites were found in lower frequencies and abundance than those found by Tschapka and Cunningham (2004) on La Selva *Calyptrogyne ghiesbreghtiana* inflorescences. The difference in mite populations between these two sites may be due to many reasons. Abiotic differences in sites such as altitude, seasonality and weather as well as biotic interactions between species may be responsible for differences in occurrence of this interaction mite, bat and plant.

La Selva Biological Station is located on the Atlantic slope, encompassing Holdridge Life zones of Tropical Wet Forest and Tropical Premontane Wet Forests, with an annual rainfall of 3,991 +/- 728 mm (n = 22 years) and ranging over elevations of 35 to 150 m (Janzen 1983). Although La Selva experiences a distinct dry season, every month receives a minimum of 150 mm of rainfall (Lesica and Antibus 1990). In fact rainfall at La Selva, as in much of the Atlantic slope forests, is so well distributed throughout the year that it is considered to have an aseasonal climate (Haber 2000).

This study was conducted in Cloud Forest on the Pacific slope of Costa Rica. The Monteverde Cloud Forest Preserve is found in a lower montane rainforest that receives an average of 3,000 mm of precipitation per year (Lesica and Antibus 1990). Site 1 in this study was located at 1520 m of elevation. Similarly, the Estación Biológica de Monteverde and site 2 are located at a higher elevation of 1600 m, and found in a lower montane wet forest life zone. Although clouds and mist are frequent throughout the dry
season, Pacific slope forests express higher seasonality than Atlantic forests (Haber 2000).

Elevational differences between sites is unlikely to be important to mite colonization considering hummingbird flower mites are found in normal communities and frequencies in both Monteverde and Cerro de la Muerte (Colwell 1983).

The major differences between the study conducted by Tschapka and Cunningham (2001) and this study is the location of collection sites in relation to the continental divide and seasonality differences that go along with this. In Monteverde minimal flowering activity occurs during the heaviest months of rainfall, September and October as well as during the windy-misty season of November and December (Haber et al. 1995).

Inflorescence stage surveys in the month of November indicate that at the time of mite census gathering both survey sites experienced a local minimum in budding and flowering inflorescences (Figures 3 and 4). Plant stage surveys over both sites indicate that most plants were not in flowering stage (Figures 1 and 2) and were in fact not producing inflorescence stalks at all, or that inflorescences were still covered by bracts. The unavailability of flowers may impose a restriction on both colonization and growth rate of mites. In addition, mature flowers may not occur at great enough abundances to cause fruit and/or nectar bats to devote foraging behavior to *C. brachystachys*. Koptur et al (1988) did a survey of seasonal penology of *C. brachystachys* in the Monteverde, finding continuous leafing, different annual periodicity, unsynchronized individuals within species.

In addition to peak and lag periods present in *C. brachystachys* phenology, *Artibeus* bat activity in the Monteverde region is also very seasonal. Absence of a phoretic carrier would prevent mites from accessing resources and therefore colonize.

Heavy precipitation in both rain and mist are part of the local weather here in Monteverde and may affect local pollination and pollinator activity.

Two different populations of the mite, *Proctolaelaps lobata*, phoretic on Lepidoptera (Insecta) and specific to *Lantana spp.* (Verbenaceae) flowers were found by Boggs and Gilbert (1987) to have remarkably different annual population dynamics in response to differences in geographic seasonality. *Lantana spp.* are distributed from Central America to Texas and the mites are assumed to follow an analogous range. Populations of *P. lobata* were studied in Santa Rosa, Costa Rica, where *Lantana spp.* flower continuously and in Austin, Texas, USA where *Lantana spp.* are dormant during the winter. Due to monophagy of *P. lobata*, an annual local extinction occurs each winter in Texas. Although *Lantana* begins to flower in Texas in April, mites are not observed until June. Soon after, density and distribution grew quickly to equilibrium within a week (Boggs and Gilbert 1987). This time of year coincides with both the year’s first annual Southerly winds and the import of commercially cultivated *Lantana* flowers. Boggs and Gilbert (1987) concluded that populations in Austin are a result of annual re-colonization of local phoresy on wide ranging insects, but could not rule out anthropogenic import.

While this bat-flower-mite commensalism relationship has been found to be widespread, more seasonal habitats are more difficult for steady populations to exist. Furthermore, seasonal populations may experience extreme minima due to seasonality of both host plant and phoretic carrier. A similar pattern to *Lantana* mites in Texas of complete re-colonization following temporary extinction each year is likely to explain
why densities and frequencies of phoretic bat mites were found to be so low on *C. brachystachys* in Monteverde. Far ranging *Artibeus* bats may annually introduce mites from the nearby Atlantic slope. This would explain the presence of mites, however in very low numbers.

Further studies concerning flowering phenologies need to be conducted over longer time periods. Foraging behavior of *Artibeus* bats and any differences of these between Pacific and Atlantic slope sites should also be explored.

**FIGURE 5.** Phoretic mite on *Calyptrogyne brachystachys* inflorescence.
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LITERATURE CITED


